III. *On the Biology of* Sphodromantis guttata (Mantidae).

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Plates VII–X.

The following paper includes some observations on the hatching, breeding and oviposition of *Sphodromantis guttata*, Thunb. (= *Hierodula bioculata*, Sauss.), and some criticisms of several of the hitherto published works on this subject. It is recognised that there are still many doubtful points on which further work is required, but, as there seems to be no probability of our being able to continue on this subject in the near future, we thought it best to put forward the present notes without any further delay.

The oothecae were collected by P. A. Buxton at El Kantara, S. Algeria, in April 1913. They were found on stones, sticks, bushes, etc., and were quite common in the little dry watercourses ("oueds") in the stony desert. Some of the larvae emerged before they were brought back to England, as early as April 19. Although no adult Mantids were seen they were probably there, as they are found at this time of the year in Egypt (Adair, 1914, i, p. 126).

A short account of the structure of the ootheca will be found below in connection with its construction. For the present it will be sufficient to recall the fact that the eggs lie in groups in the middle of a case, and that each group of eggs has a passage to the exterior along which the just-hatched larvae pass.

Emergence generally took place in the morning, a large number of young appearing almost simultaneously, followed by stragglers for a few hours, and further batches from the same ootheca on the following days. Several authors have commented on this simultaneous hatching of a number of eggs, and the remarkable spectacle of the dozens of young emerging from the ootheca. It is probably brought about by the vibration made by one larva as it emerges, exciting the larvae in the neighbouring eggs. We have noticed in other insects * that eggs may be ready to hatch and yet wait for some external stimulus. That all the eggs do not mature at the same moment is shown by emergence occurring on several successive days from the same ootheca.

The Mantis larvae invariably made their appearance head first; emergence was rapid, but there was a slight pause after the head and thorax had protruded from beneath the flap on the dorsal surface of the egg mass. Then the head was jerked backwards and the larva freed itself suddenly. It was unable to use its legs, and hung down over the edge of the ootheca on a double thread, which in some specimens was as much as two inches long. Brongniart (1882, p. 450) states that they hang in this position for some days; while Giardina (1899, p. 324) considers that those which remain hanging for long invariably die, and that normally they leave the ootheca by "breaking the filaments" at the entrance of the passage. All those under our observation hung down for a few minutes on the end of the thread and then moulted, as will be described later. In no case were the threads broken, but remained attached to the empty skin.

A larva removed from the egg just before hatching is shown in Plate VII. It is about 4·5 mm. long, and the prothorax is shorter than the head (prothorax ·68 mm; head ·84 mm., measured dorsally). The head is not bent down on to the surface of the meso- and meta-sternum as described and figured in a Chinese species by Waterhouse (1912, p. cxxvi), but the two lateral projections of the head which bear the eyes are pressed diagonally (not folded) back against the sides of the prothorax. The larva emerges from the ootheca in this condition, except that in the passage along the exit tunnel the legs and antennae become unfolded and stretch out behind. On emergence it is yellow with paler limbs and dark greenish blue eyes; there are red spots at each femoro-tibial joint, and also mid-dorsally on each thoracic tergite.

On the anterior portion of the head the chitin is thickened,

* On one occasion when examining some eggs of a *Raphidia*, no sooner had they been disturbed from their original habitat and placed on a slide for examination than they all hatched. (Williams, C. B., "Entomologist," 1913, p. 7.)

forming a protective shield, or plate, which ends dorsally and ventrally in a pointed prolongation (Pl. VII, fig. 1*a*). The sides of this are reticulated for a short distance, and it is this reticulation that was apparently mistaken by Pagenstecher (1864) for the covering of the eyes (" augenflecken "). This plate may possibly be used in breaking open the egg.

On the ventral surface at the posterior end are two pairs of small papillae, one pair on the hind margin of the ninth sternite and the other beneath the sides of the posterior margin of the tenth tergite. The posterior pair (*c*) secrete the two threads by which the larva hangs from the ootheca. These threads frequently unite a short distance behind the larva, forming a flat band. Brongniart (1882, p. 451) states that one thread is attached to each end of the eggshell. This, however, is not so, as in sections of ootheca which expose empty eggshells, both threads can be seen entering the shell, and are attached to its interior surface near to the posterior end.

It is remarkable that we were able to draw out a considerable length of thread (2–3 mm.) from the papillae of a cast skin. Whether the whole thread-forming apparatus is cast with the skin we have not been able to decide, but it should be noted in this connection that at no other stage in the life of the Mantis is any thread or silk produced. According to Giardina, Pawlowa (1896) studied the development of the thread and found that it was formed from a mass of cells arranged in a single spiral series which take the form of a cellular filament. This undergoes morphological and chemical change until it loses all cellular structure and is reduced to a fine but resisting thread. We have been unable to consult Pawlowa's or ginal work.

Pagenstecher (1864, p. 13) and de Saussure (1872, p. 223) describe the presence of a number of backwardly directed spines on the abdomen of the just-hatched larva, by means of which they are enabled to work their way up the passage from the egg to the exterior, according to the latter " de la même manière qu'un epi de seigle, à l'aide de barbes à ergots, peut cheminer sur un morceau de drap soumis à des vibrations." Brongniart (1882, p. 450) denies this, and states that the spines on the body are confined to the cerci, and also remarks that the spines on the legs assist in the exit. Recent authors have unfortunately tended to follow Brongniart, and his statement appears in most text-books. We find, however, that the two former writers were correct, and that the tergites of the meso- and meta-thorax and of the abdomen are covered, except for a narrow dorsal line; with a number of very minute backwardly directed flattened spines. These are broader and with an enlarged base towards the anterior margin of each tergite, particularly those of the thorax, and become narrower and longer towards the posterior margin (text fig. 1, A and B and Pl. VIII). They are also present on the labrum. The spines are only 8–12 μ long, and are best

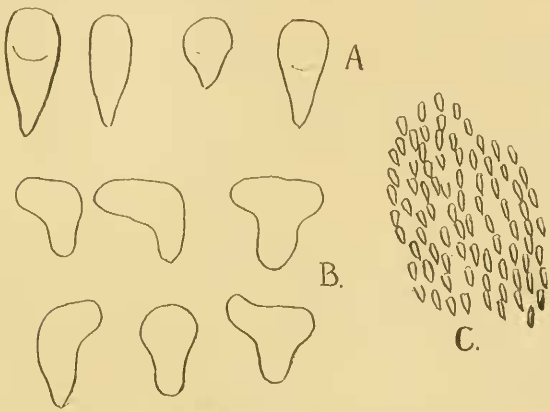

FIG. 1.—Spines on tergites of first larva.

A. Near posterior margin of abdominal tergites.
B. Near anterior margin of thoracic tergites.
C. Portion of abdominal tergite less magnified.

seen in stained preparations of the cast skin under a high magnification. There are also four rows of much larger spines on the silk-producing papillae.

These spines have been found in a number of other species, including *Mantis religiosa*, *Stagmomantis carolina*, *Stagmomantis limbata*, and in several species of which we have been able to get a few dried cast skins still attached to old unidentified oothecae. There is no doubt that they will be found in all Mantidae.

We find also that all the distinctly visible spines on the legs (Pl. VII, fig. 1*d*) are *beneath* the first skin and are seen through it; they can therefore be of no service in emergence. It is probable that the young larva moves along the passage by a series of telescopic expansions and contractions of the abdomen, rather than by a simple wriggling movement as de Saussure seems to imply in the remarks quoted above.

It is important to notice that the legs and antennae of the first-stage larva are free from the body, and that the skin, which is soon to be cast, envelops each limb separately. Several observers have made the mistaken observation that the skin enclosed the animal as a whole, pressing the legs and antennae against the body. They have assumed this from an examination of cast skins, in which the envelope of each leg becomes completely telescoped upon the base on the withdrawal of the leg, and is not obvious in a cursory examination. On Plate VIII are shown two microphotographs of a cast skin. In one the skins of the legs and antennae remain telescoped as left by the larva, and are very inconspicuous; in the second the leg skins have been drawn out before the specimen was mounted.

There has been much controversy as to the morphological status of this first skin, which is cast almost immediately after emergence. Most authorities have persisted in regarding it as an amnion, being misled by the idea which we have just corrected, that it encloses the whole insect like an eggshell, and also by Brongniart's statement that no spines are present on its surface. Pagenstecher's figure (1864, Pl. I) which showed these, and which is the best figure of the cast skin yet published, has even been designated as "fanciful" by Packard (1898, p. 584). However, in view of the observations stated above—namely, that it has a number of spines on the abdominal and thoracic tergites; that it envelops individually the limbs and the antennae; and that the threads from the end of the abdomen pass through it, and, further, from the fact that it is resistant to boiling in potassium hydroxide, and that its staining properties are similar to those of chitin—we have no doubt that it is a true skin and not an amnion.

Six and a half minutes after the first appearance of the larva the skin split mid-dorsally, and three minutes later the larva was completely free and fell soft and helpless to the ground. The limbs left the skin after most of the trunk was free; first the anterior pair, and then the two posterior pairs and the antennae almost simultaneously.

Finally the tail was freed. This is only accomplished with difficulty if the insect is hanging free of all foothold. If, however, it is lying on or against something solid, the following method is employed. The insect, lying on its ventral surface, strains away from the old skin, which is bound to the ootheca by the thread, applying leverage to the surface on which it rests by means of the joint at the trochanter. It moves the tail round in circles in such a way as to keep the threads stretched. After some effort the abdomen is finally freed from the old skin, which remains hanging on to the ootheca attached by the two threads. This is usually completed about nine or ten minutes from the first appearance of the larva.

The larva has now changed considerably in shape; the abdomen is longer, and for a few minutes lies straight out behind it on the ground; the sides of the head have spread out owing to their being no longer confined by the first skin, and the head assumes the typical hammer shape; the prothorax has elongated, and is now much longer than the head (head 1 mm., prothorax 1·8 mm.). The larva now lies motionless on the ground for some minutes. During this time the abdomen is shortened telescopically, and is cocked up over the back to the position which is normally retained till the end of larval life. Finally, after about ten minutes' rest, the skin has hardened and the larva can run about actively. The colour is matured in about two hours, during which a general darkening is observed, especially of the legs and the dorsal surface of the body. The colour at this stage, however, is no indication of that of the adult, as changes occur in larval and, according to Przibram (1906, pp. 203 and 206), even during adult life.

The larvae, now in their second instar, are very active. They can jump as much as two and a half inches, the second and third pair of legs alone being used in this, as also in slow walking; in running, however, all three pairs are used. They frequently sway from side to side for some minutes while standing still, recalling a similar habit in the related *Phasmidae*.

Some of the larvae were fed on aphis, as it was the most easily obtainable food at the end of April. When they had captured one they rotated it with the end of the disengaged tibia until they were able to bite it at the back of the thorax. This treatment paralysed the prey rapidly, and it was then consumed. Other specimens would not eat aphids, but having captured them threw them aside. From these and from contradictory records of other authors it seems probable that either different aphids are attractive in different degrees, or that this Mantid will only take them when it is without other more palatable food.

The following method of feeding the young Mantids was devised, and could be applied to the feeding of any small predaceous or insectivorous animals. Insects of every description were collected in a very fine mesh net by sweeping hedges, grass, growth along a ditch side, etc. The net was then turned inside out into a beaker. If this was done indoors, with the bottom of the beaker towards the light, very few flies escaped. Finally, the beaker was covered with a piece of coarse net and placed in the cage containing the larvae. All the smaller insects in it rapidly escaped through the net into the cage, while the larger ones, spiders, etc., were kept inside the beaker. In this way *Aleyrodes*, *Coniopterygidae*, Cercopids, Jassids and many small Diptera were supplied in numbers and eaten. The mesh of the net covering the beaker was increased as the Mantids grew, until finally they were able to take any insects obtainable.

Several times when the sun was shining on the cage the young larvae were observed on the back of the cage following and repeatedly attempting to capture the shadow of a fly moving on the glass front. This indicates that their sense of smell is not highly developed.

The insects lived throughout the summer, some in a hothouse (average temperature about 75°), some in a living-room; while others even survived a trip for a few days to an altitude of 3000 ft. in Norway. They are apparently extremely hardy.

As the larvae become older their habits change; the half-grown larva never jumps, and rarely stalks its prey, preferring to capture such insects as happen to approach it. More carelessness in feeding is also observed; legs and wings of the prey are frequently dropped, and sometimes the unconsumed portion of a fly is allowed to make its escape; the larvae also are no longer so particular in attacking their prey behind the head, but commence their meal at any convenient part, abdomen, head or even wings. When they were older their chief food was house flies (*Musca*) and bluebottles (*Calliphora*), but they would also eat wasps, Syrphids, small Heteroptera and grasshoppers. They appeared somewhat afraid of butterflies, but when hungry attacked them. They would not eat caterpillars, and showed a strong dislike to Tipulids and Coccinellids. It is possible, however, that these are unmanageable rather than distasteful. A half-grown nymph consumed a whole bluebottle in $11\frac{1}{2}$ minutes. Occasionally one would capture one fly while still eating another, in which case the second fly was retained under the free arm till the first was finished. One larva was observed to take up a fly which had been dead some days and had dried up; nevertheless, with great difficulty it was devoured completely. On another occasion one was seen biting pieces off some dry hawthorn leaves. All the stages readily drank drops of water, and doubtless in the wild state are in the habit of sucking up the dew.

Cannibalism rapidly reduced the number of larvae, and soon only a very few were left. Sometimes a fight would be started by accident. Thus, in one case, a larva in striking at a fly caught the tail of a smaller larva and bit off one of the cerci. The latter retaliated by removing both antennae from the larger individual. Although they were separated, the smaller one was found partially devoured on the following day.

On September 2 a full-fed nymph cast its last skin and became an adult female. This fed on miscellaneous insects until October 24, when it made its first ootheca.

Oothecae, which differ greatly in different species, have been frequently described—*Mantis religiosa* by Pagenstecher (1864) and Giardina (1898 and 1899); *Hierodula saussurii* by Kershaw (1907); *Stagmomantis carolina* by Rau (1913); *Miomantis savignyi* by Adair (1914, i and ii); *Fischeria baetica* by Adair (1914, ii); *Sphodromantis guttata* (*bioculata*) by Adair (1914, ii); *Gongylus gongyloides* by C. E. Williams (1904); and unidentified species by Shelford (1909) and by Waterhouse (1912). The most complete account is that of Giardina (1899), with whose conclusions, however, we cannot entirely agree.

It will be convenient here to give a short account of the ootheca of *Sphodromantis guttata*, in order that the operations of the female described below may be better understood. Transverse, longitudinal vertical and longitudinal horizontal sections are shown in text fig. 2, I, II and III, and the letters below refer to these. The ootheca consists of a central core containing the eggs C, surrounded by a protective layer D, and separated from it, laterally and ventrally, by a stout irregular wall F. The central part is divided by transverse vertical lamellae G into a number of flat chambers, each containing a group of eggs. Each chamber is roughly semicircular, being closed at the middle line (I), and the chambers on each side alternate (III). Each compartment communicates with the exterior by a passage (A and B) leading from the eggs to the dorsum of the ootheca, where it opens between the successive members of a series of flaps H. Within each opening there is a protective flap E, arranged as a valve, so that it can be pushed aside from within but prevents entry from without. The vertical divisions between the egg-chambers continue, less stout in structure, across the outer protective layer D, and are indicated on the exterior by a series of vertical furrows on the sides of the ootheca M. A few chambers at each end of the ootheca are without eggs, and act only as protection. Giardina (1899, p. 296) considers the transverse walls between the egg-chambers to consist of three layers closely pressed together, but we could see no evidence of this; they tend to split in places, but quite irregularly.

The whole ootheca is formed of a gumlike substance secreted from large abdominal glands, which open into the oviduct. This gum, which hardens on exposure to air after being secreted, is partly vacuolated into a kind of froth by the gonopophyses as it passes from the body. That portion which goes to form the outer protective layer is still more vacuolated afterwards.

The construction of the first ootheca laid by the female started about one o'clock in the afternoon, and by two o'clock, when it was first observed, about one-quarter had been completed. The insect was head downwards on the perforated zinc side of the cage, and was so engrossed in the process that, even when the cage was broken to pieces in order to get a better view, it was not in any way disturbed. The elytra were slightly raised and quite clear of the ootheca, and only the very tip of the abdomen was immersed in the froth, at certain times as far as the base of the cerci, which, however, were always quite free and were employed in feeling the surface under construction.

The use of the elytra in the formation of the ootheca has been affirmed and contradicted many times. There is no doubt whatever that the ootheca can be constructed

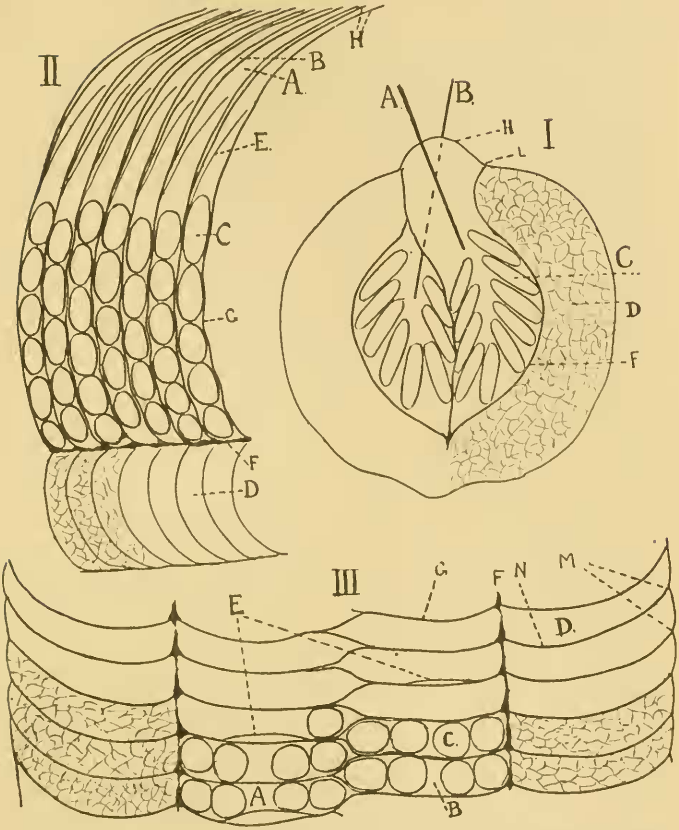

FIG. 2.—Portions of sections of ootheca of *Sphodromantis guttata.*

I. Transverse.
II. Longitudinal vertical.
III. Longitudinal horizontal.
A and B. Passages entering successive egg chambers.
C. Egg.
D. Chamber of outer protective layer.
E. Protecting flap in passage.
F. Outer wall of central portion containing eggs.
G. Transverse partition between successive chambers.
H. Dorsal flaps between which egg chambers communicate with the exterior.
L. groove at each side of dorsal flaps.
M. Vertical furrows on outer surface indicating position of transverse partitions.
N. Portion of transverse partition traversing protective layer (D).

without their aid. The photographs (Pl. IX and X) show the position in which the Mantis remained during the whole process, and Adair (1914, I, p. 120) cut off the wings of one specimen which was laying its eggs, in order to get a better view, without disturbing the Mantis or the construction of the ootheca. In view, however, of the definite statements of Brongniart (l.c., p. 449), Perrier (1870) and Giardina (1899, p. 311), it seems possible that occasionally the elytra may assist. In any case, the view of Perrier and Giardina that the longitudinal furrows on each side of the dorsal flaps are due to the pressure of the elytra is unsound, and still more so the ingenious theory of the latter author, that the exit passage and protective flap are formed by the insertion of the elytra and hind-wing, for our ootheca, constructed entirely without their aid, has all these features in a normal condition. It occurs to us that when the insect is upside down the wings might be used to prevent the freshly secreted material from flowing away, but even at this stage it is not very liquid.

In the construction of the ootheca the tip of the abdomen goes through a regular cycle of movements, each repetition resulting in the laying of one group of eggs and the formation of the corresponding portion of the ootheca.* This cycle is shown diagrammatically at text fig. 3, which represents the face of the ootheca under construction (seen from the direction of the insect). This face is not flat but concave, being most sharply curved in a vertical plane, as may be seen in the partially constructed ootheca in Pl. X, 1, and also in sections of the completed ootheca, text fig. 2, II, by the curve of the divisional wall. The movements are as follows: When the insect has finished laying a group of eggs at A, on the left-hand side, the tip of the abdomen is moved with a slight curve to the top of the right-hand side of the ootheca, and then slowly down to the bottom along the periphery. During this movement the gonopophyses may be seen moving rapidly backwards and forwards just beneath the slightly hardened outer skin. By this process the gum in the outer layer is more vacuolated, the divisional transverse wall N in this area formed,

* Giardina (1899, p. 147) states that all the eggs and thecal material on one side of the ootheca are secreted by the corresponding ovary and colleterial gland. He gives no evidence for this, and we saw nothing in the construction that would necessitate this assumption.

and by stretching the outer surface with the tips of the gonopophyses the vertical ridge, or swelling, is formed, which is seen on the exterior alternating between the lines of the vertical divisions. During the downward movement a fresh supply of secretion is left behind on the right half of the face of the ootheca. The movement continues to the base, where an addition is made to the length attached to the support. Then the abdomen is inserted more deeply, up to the base of the cerci, into the centre of the right side of the ootheca at B, and remains comparatively quiet for about two minutes. During this time the group

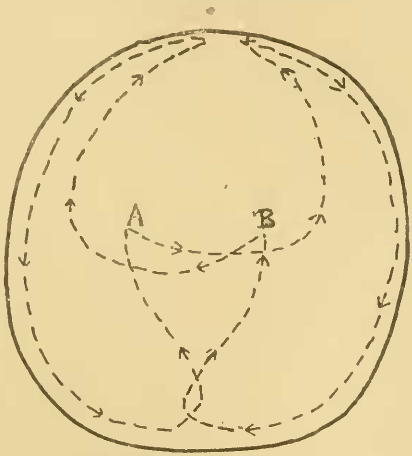

Fig. 3.—Diagram of movements of abdomen of female. For explanation see text.

of eggs on this position is laid, and the walls of the compartment are formed by compressing the only partially vacuolated material displaced by the eggs. The abdomen then becomes more active and is once more moved in a curve, as shown, to the upper point of the left-hand side, where the slow downward movement once more begins.

The process of laying one group of eggs and the corresponding part of the ootheca occupies about four and a half minutes, and, as each side is formed alternately, there is an interval of about nine minutes between successive repetitions of the same operation on the same side. (Actual times measured were 9, 9, 9, 8, 7 minutes; the times would be less at the commencement and finish, as the ootheca tapers off at each end and fewer eggs are laid in the earliest and latest compartments.) Thus the constructed portions on one side have had this time to harden before the next compartment on the same side is formed, and the pressure of some of the freshly secreted material against that which has already partially hardened results in the formation of the cross divisions.

The formation of the dorsal flaps and the protecting valve is still somewhat obscure. It must take place just before the descending movement, as only at that time is the tip of the abdomen at the dorsal part of the egg mass. Further observation on this point is needed. When the ootheca is first constructed there is not direct communication with the exterior, but the passages between the flaps are filled with a very delicate dried froth. The young Mantis on hatching pushes through this and breaks it up. In those compartments in which all the eggs have been parasitised this dried froth persists.

The construction was finished at 4.45 p.m., having occupied about three hours and forty-five minutes. The colour of the material when first exuded was very pale, but it rapidly darkened on exposure, so that before the completion of the ootheca the first-made portions were much darker than the more recent part.

On November 27 another ootheca was constructed by the same female, this one being much smaller than the first; probably, however, this was only due to insufficient feeding, as Adair (1914, p. 126) finds as many as six successive ootheca laid by one individual of this same species, and a dissection of the above female, which died on December 9, showed many eggs still in the ovaries.

The female had not paired, so that the eggs were infertile. Examination has shown that they have all dried up, so that parthenogenesis, so common in the allied *Phasmidae*, apparently does not occur in this Mantis.

Some notes on the Chalcid *Podagrion pachymerum*, which infested some of the oothecae brought back from Algeria, have already been published (Williams, C. B., 1914).

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EXPLANATION OF PLATES VII–X.

PLATE VII. Larva of *Sphodromantis guttata* extracted from the egg.

FIG. 1. Ventral view. *a.* head shield; *b.* papillae on 9th sternite; *c.* thread producing papillae on 10th abdominal segment; *d.* spines on leg *beneath* the first skin; *md.*, mandible; *lab.*, labrum; *mx.*, maxillae; *mx. p.*, maxillary palps.

FIG. 2. Lateral view.

PLATE VIII. Microphotographs of first cast skin of larva; magnified 24 diameters.

The spiny areas and terminal papillae are shown. In fig. 1 the skin is shown as cast; in fig. 2 with the coverings of the legs pulled out.

PLATE IX. Lateral view of female *Sphodromantis guttata* constructing ootheca. Ootheca nearly complete. Natural size.

PLATE X. Lateral and dorsal view of female constructing ootheca. Ootheca about half completed. Slightly reduced.